

## A complex of putative acanthocolpid cercariae (Digenea) from *Nassarius olivaceus* and *N. dorsatus* (Gastropoda: Nassariidae) in Central Queensland, Australia

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### Abstract

*Cercariae capricornia* I–VI, six new cercariae putatively identified as belonging to the Acanthocolpidae, are described and named from prosobranch gastropods of the family Nassariidae collected from the intertidal zone in the Capricornia region, Central Queensland, Australia. Four species are reported from *Nassarius olivaceus* and two from *N. dorsatus*. The cercariae have a unique and complex three-dimensional body shape, including a keel, which differentiates them from previously described acanthocolpid cercariae. These are the first cercariae to be described from these gastropods.

**Key words:** *Cercaria capricornia*, Capricornia, Acanthocolpidae, *Nassarius dorsatus*, new species, gastropod parasites

### Introduction

Several authors have described large oculate cercariae that have generally been considered to belong to the Acanthocolpidae: *Cercaria caribbea* XXXIV Cable, 1956, *C. portosacculus* Holliman, 1961, *C. caribbea* LXXII Cable, 1963, *C. caribbea* LXXIII Cable, 1963, *C. itoi* Shimura, 1984 and a probable *Tormopsolus* cercaria (Bartoli & Gibson 1998, Cable 1956, Cable 1963, Holliman 1961, Shimura 1984). These cercariae were reported from marine gastropods of the families Buccinidae, Columbellidae and Fasciolariidae, all belonging to the Muricoidea. Here, we report a complex of comparable but distinct cercariae from another muricoid family, the Nassariidae.

The marine gastropods *Nassarius olivaceus* (Bruguière) and *N. dorsatus* (Röding) are common scavengers in the intertidal mangroves of the Capricornia region in Central Queensland, Australia. *Nassarius olivaceus* is found in the mid intertidal zone, amongst mangroves and ranging out into adjacent inundated areas, while *N. dorsatus* is predominantly found in the low intertidal zone. *Nassarius olivaceus* is distributed from Darwin, Northern Territory, across northern Australia to Moreton Bay in south-eastern Queensland, while *N. dorsatus* is distributed north from Exmouth Gulf in Western Australia, across the Northern Territory and Queensland to northern New South Wales (Wilson 1994). The trematodes reported here are the first from these gastropod species and the first larval digeneans reported from mainland Capricornia.

## Material and methods

Molluscs were collected by hand from mudflats at Sandy Point, Corio Bay ( $22^{\circ}58' S$ ,  $150^{\circ}46' E$ ), Ross Creek, Yeppoon ( $23^{\circ}8' S$ ,  $150^{\circ}45' E$ ) and the mouth of Cawarral Creek, Keppel Sands ( $23^{\circ}19' S$ ,  $150^{\circ}47' E$ ) in Central Queensland, Australia. A total of 1908 *N. olivaceus* and 1766 *N. dorsatus* were collected between August 2004 and May 2006. Molluscs were held in filtered seawater at room temperature ( $20\text{--}28^{\circ}\text{C}$ ) and examined for naturally emerged cercariae every 1–3 days for up to one month. Freshly emerged cercariae were transferred to a cavity block in a small volume of seawater and heat-killed by pouring several volumes of near boiling seawater into the dish, fixed in 5% formalin or 70% ethanol without flattening and examined as temporary wet mounts. Cercariae with exaggerated curvature of the forebody were slightly flattened by reducing the amount of water under the coverslip. Live specimens were also observed as wet mounts. One or more infected molluscs were dissected to determine the nature of intra-molluscan stages for each cercarial species. Rediae were placed into near boiling seawater, fixed in 5% formalin and examined as temporary wet mounts. Measurements were taken using an eyepiece micrometer on an Olympus BX-41 microscope and are given in micrometres as the range followed by the mean in parentheses. Standard deviations were calculated where more than 30 measurements were taken. Drawings were prepared with the aid of a drawing tube. A subset of putatively uninfected molluscs was dissected to confirm the absence of infection. Of 399 *N. olivaceus* (20.9%) and 556 *N. dorsatus* (31.5%) dissected, there was just one *N. dorsatus* infected with a trematode similar to those described here, but the cercariae were too immature for morphological comparison. This result suggests that the emergence prevalence closely approximates the actual prevalence. Representative wholermounts stained with Mayer's haematoxylin, cleared in methyl salicylate and mounted in Canada balsam and all wet specimens are deposited at the South Australian Museum.

## Results

Six distinct cercariae with complex body shapes emerged naturally from these gastropods, four from *N. olivaceus* and two from *N. dorsatus*.

### *Cercaria capricornia I*

(Fig. 1)

**Host:** *Nassarius olivaceus* (Bruguière) (Gastropoda, Nassariidae).

**Locality:** Ross Creek, Yeppoon, Queensland ( $23^{\circ}8' S$ ,  $150^{\circ}45' E$ ).

**Habitat:** Amongst and immediately adjacent to mangroves on intertidal mudflats.

**Other locality:** Cawarral Creek, Keppel Sands, Queensland ( $23^{\circ}19' S$ ,  $150^{\circ}47' E$ ).

**Prevalence of emergence:** 0.16% (3 of 1908 *N. olivaceus*).

**Material:** South Australian Museum, AHC 29306–AHC 29307, AHC 34513–AHC 34517.

**Dates of collection:** May 2005 and February 2006.

#### Description:

Redia

*Site.* Reproductive and digestive glands.

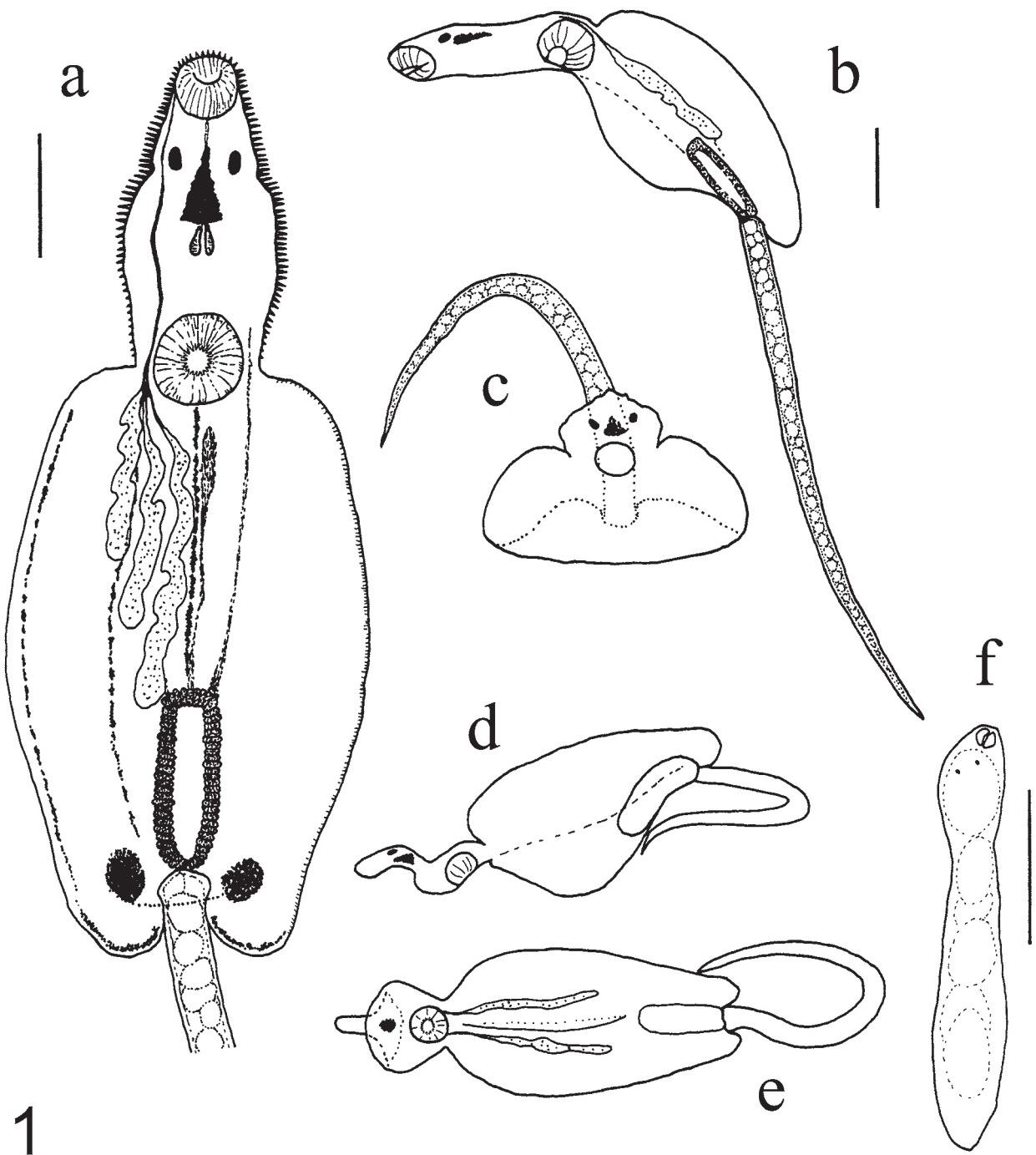
*Structure.* Body elongate, cylindrical with posterior extremity tapering, rounded (Figure 1f). Mouth opens terminally; pharynx spherical. Cercariae in various stages of development.

*Dimensions.* Based on 10 unflattened rediae.

Length: 400–580 (478.0)

Width: 65–120 (89.0)

Pharynx: 20–28 (23.3) x 20–25 (23.5)



**FIGURE 1.** a-f. *Cercaria capricornia* I naturally emerged from *Nassarius olivaceus*: a. Body, heat-killed, in ventral view; b. Entire cercaria, heat-killed, from side view; c. Live cercaria, body folded for swimming, from dorsal view; d. Live cercaria, resting attitude, side view; e. Live cercaria, resting attitude, ventral view; f. Rediae, fixed, containing cercariae at different stages of development. Scale bars a, b = 100  $\mu\text{m}$ ; c-e not to scale; f = 200  $\mu\text{m}$ .

#### Naturally emerged cercaria

**Body.** Flattened, with conspicuous constriction at level of ventral sucker (Figure 1a). Forebody reduced, slender, arched ventrally, widening medially. Hindbody posterior to constriction expanded, large, broadly ovate, extremely flattened, extending beyond tail junction on both sides, with deep ventral keel longitudinally between constriction and anterior extremity of excretory vesicle; ventral margin broadly rounded in profile (Figure 1b). In life, forebody reflexed dorsally at

ventral sucker and curved ventrally, fleshy portion around ventral sucker expanded; hindbody slightly arched dorsally; sides reflexed dorsally on either side of keel in V formation (Figures 1d, 1e).

*Tegument.* Spines anterior to constriction, arranged in regular rows in anterior forebody, longest in anterior half forebody, decreasing in size towards constriction.

*Suckers.* Oral sucker opening ventrosubterminally, spinose, lacking stylet. Ventral sucker round; aperture surrounded by single row of approximately 76–82 inwardly facing spines.

*Eye-spots.* Oblong, dense, lateral on either side of prepharynx.

*Pigment.* Dark brown-black, dense, conspicuous, in forebody medially between eye-spots and pharynx; brown-black, diffuse, may be present between pharynx and ventral sucker; brown-black lines may be present on hindbody along ventral margin of keel and in two longitudinal lines lateral to keel on each side; golden brown, oblong, either side of tail base (Figure 1a). In life, pigment in forebody and lines on hindbody blue-black.

*Penetration glands.* Three pairs of long, elongate and folded saccular glands, extend from posterior margin of ventral sucker to excretory vesicle, longest may extend past anterior extremity of excretory vesicle; ducts run anteriorly on lateral edges of body. Central glands not evident in forebody.

*Digestive system.* Mouth opens anteroventrally. Prepharynx long, narrow. Pharynx pyriform, small.

*Excretory system.* Excretory vesicle I-shaped, cylindrical, turgid, thick-walled, with columnar cells, almost one-third length hindbody. Two lateral ducts open into anterior extremity of vesicle. Flame cells difficult to discern, formula not determined.

*Tail.* Simple, long, cylindrical, gradually tapering terminally; lacks spines, setae or fins.

*Dimensions.* Based on 86 naturally emerged specimens.

Total body length: 580–800 ( $717.0 \pm 48.6$ )

Length anterior end to tail base: 530–750 ( $665.6 \pm 45.9$ )

Maximum width hindbody: 260–360 ( $313.3 \pm 23.2$ )

Maximum width forebody: 100–155 ( $123.6 \pm 10.7$ )

Width at constriction: 75–133 ( $106.6 \pm 12.8$ )

Length forebody: 185–240 ( $215.0 \pm 13.8$ )

Oral sucker: 42–58 ( $49.3 \pm 2.8$ ) x 45–60 ( $51.7 \pm 4.0$ )

Ventral sucker: 65–88 ( $78.0 \pm 3.8$ ) x 65–83 ( $72.9 \pm 4.8$ )

Prepharynx (n=83): 120–158 ( $135.9 \pm 8.6$ )

Pharynx (n=82): 20–38 ( $25.5 \pm 3.6$ )

Excretory vesicle: 115–168 ( $141.8 \pm 11.0$ ) x 47–75 ( $56.3 \pm 5.3$ )

Tail (n=42): 690–890 ( $829.0 \pm 40.7$ ) x 30–55 ( $42.7 \pm 5.3$ )

Pigment on forebody: 35–65 ( $47.6 \pm 7.6$ ) x 20–33 ( $25.7 \pm 2.7$ )

*Cercarial emergence: rhythm and variation.* Cercariae emerged in large numbers with variable periods between emergences (few days to weeks), sometimes emerging on consecutive days; emergence generally between 7 pm and 8 am.

*Behavior.* Naturally emerged cercariae are free-swimming and swim actively toward light where they orient themselves facing away from the light source. When swimming, the hindbody is folded ventrally and the forebody is highly contracted longitudinally (Figure 1c); the tail lashes from side to side for movement. When resting, the hindbody is slightly flexed dorsally; tail extending backwards and angled ventrally from hindbody (Figure 1d). When first emerged, cercariae swim actively towards light and frequently rise to the surface after which they settle on their side or ventral side up. After about 24 hours cercariae become less active, decaudation may occur and they start to die. The cercariae never encyst.

***Cercaria capricornia* II**

(Fig. 2)

**Host:** *Nassarius olivaceus* (Bruguière) (Gastropoda, Nassariidae).

**Locality:** Cawarral Creek, Keppel Sands, Queensland (23°19' S, 150°47' E).

**Habitat:** Amongst and immediately adjacent to mangroves on intertidal mudflats.

**Other localities:** Sandy Point, Corio Bay, Queensland (22°58' S, 150°46' E), Ross Creek, Yeppoon (23°8' S, 150°45' E).

**Prevalence of emergence:** 1.26% (24 of 1908 *N. olivaceus*).

**Material:** South Australian Museum, AHC 29308–AHC 29311, AHC 34518–AHC 34548.

**Dates of collection:** August/November 2004, February/May-June/August/November 2005 and March/May 2006.

**Description:**

Redia

*Site.* Reproductive and digestive glands.

*Structure.* Body elongate, cylindrical with posterior extremity tapering to point (Figure 2f). Mouth opens terminally; pharynx spherical. Cercariae in various stages of development.

*Dimensions.* Based on 12 unflattened rediae.

Length: 290–420 (344.2)

Width: 50–100 (72.5)

Pharynx: 17–33 (22.9) x 17–30 (22.1)

Naturally emerged cercaria

*Body.* Flattened, with conspicuous constriction at level of ventral sucker (Figure 2a). Forebody reduced, slender, arched ventrally, widening medially at about level of pharynx. Hindbody posterior to constriction expanded, large, broadly ovate, extremely flattened, extending beyond tail junction on both sides, with deep ventral keel longitudinally between posterior margin of ventral sucker and anterior margin of excretory vesicle; keel roughly triangular in profile, deepest midway between constriction and anterior extremity of excretory vesicle, ventral margin varies from sharp angle to broadly rounded (Figure 2b). In life, anterior end of forebody reflexed dorsally and angled forward posterior to eye-spots; hindbody slightly arched ventrally, sides reflexed dorsally on either side of keel in V formation (Figures 2d, 2e).

*Tegument.* Spines anterior to constriction arranged in regular rows in anterior forebody, longest in anterior half forebody, decreasing in size towards constriction.

*Suckers.* Oral sucker opening ventrosubterminally, spinose, lacking stylet. Ventral sucker round, aperture surrounded by single row of 71–85 inwardly facing spines.

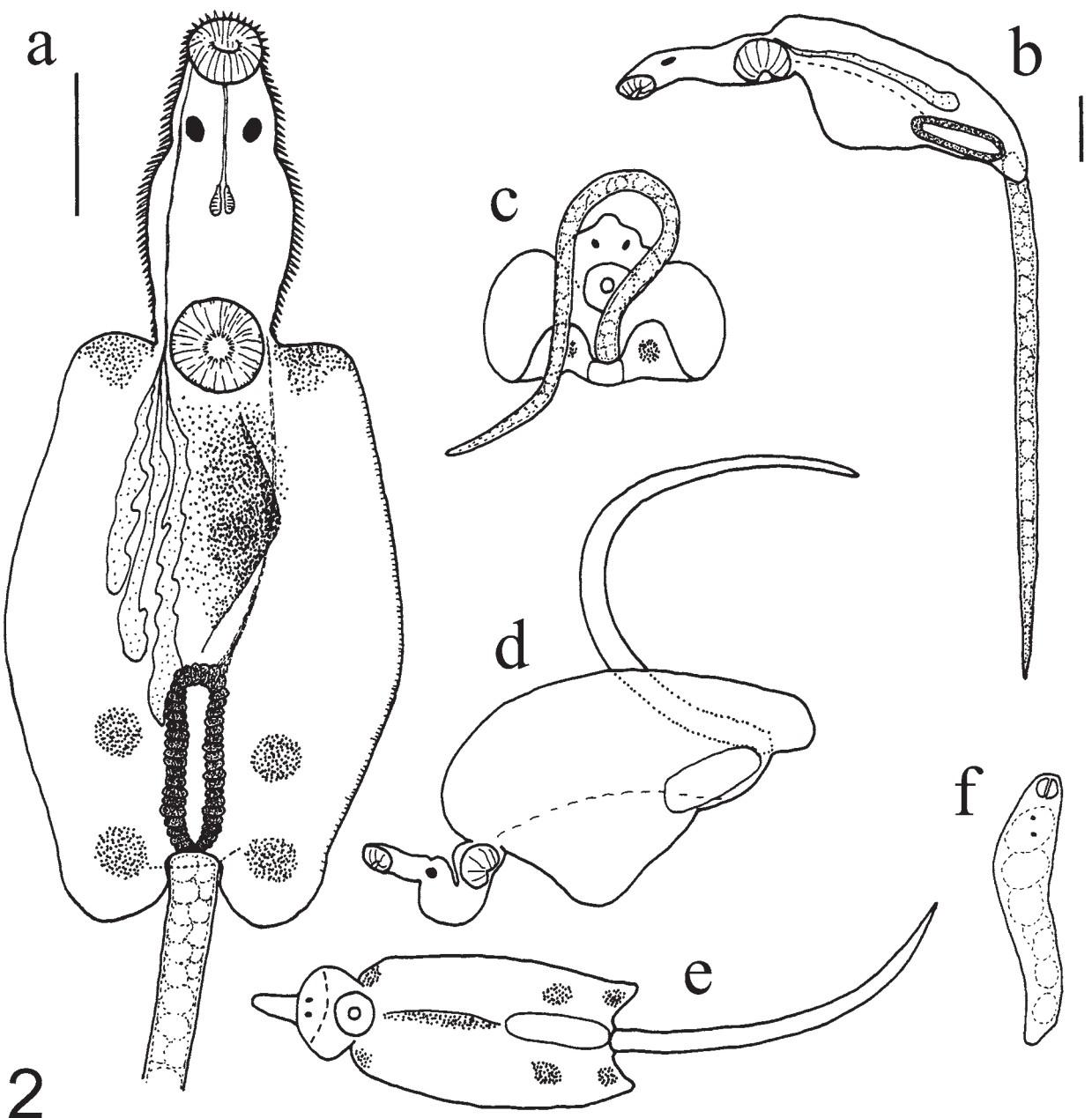
*Eye-spots.* Oblong, dense, lateral on either side of prepharynx.

*Pigment.* Golden-brown, variable: sides of keel sometimes with 4 conspicuous spots – one pair laterally each side of tail base, one pair about level with midpoint of excretory vesicle, laterally about midway between midline and margin; some with regions on anterior edge of expanded hindbody; some with region anterior to ventral sucker. In life, orange brown shading on anterior part of hindbody and keel; small orange brown spots on posterior hindbody sometimes present.

*Penetration glands.* Three pairs of long, elongate and folded saccular glands, extend from posterior margin of ventral sucker to excretory vesicle, longest often extending almost half length of excretory vesicle; ducts run anteriorly on lateral edges of body. Central glands not evident in forebody.

*Digestive system.* Mouth opens anteroventrally. Prepharynx long, narrow. Pharynx pyriform, small.

*Excretory system.* Excretory vesicle I-shaped, cylindrical, turgid, thick-walled, with columnar cells, one-third length hindbody. Two lateral ducts open into anterior extremity of vesicle, anterior extremity often obscured by glands. Flame cells difficult to discern, formula not determined.



**FIGURE 2.** a–f. *Cercaria capricornia* II naturally emerged from *Nassarius olivaceus*: **a**. Body, heat-killed, in ventral view; **b**. Entire cercaria, heat-killed, from side view; **c**. Live cercaria, body folded for swimming, from ventral view; **d**. Live cercaria, resting attitude, side view; **e**. Live cercaria, resting attitude, ventral view; **f**. Rediae, fixed, containing cercariae at different stages of development. Scale bars a, b = 100  $\mu\text{m}$ ; c–e not to scale; f = 200  $\mu\text{m}$ .

*Tail.* Simple, long, cylindrical, gradually tapering terminally; lacks spines, setae or fins.

*Dimensions.* Based on 249 naturally emerged specimens.

Total length body: 380–710 ( $553.9 \pm 63.2$ )

Length anterior end to tail base: 360–660 ( $524.7 \pm 58.3$ )

Maximum width hindbody: 212–340 ( $267.8 \pm 24.6$ )

Maximum width forebody: 75–138 ( $111.7 \pm 11.0$ )

Width at constriction: 65–133 ( $94.3 \pm 11.7$ )

Length forebody: 130–235 ( $197.4 \pm 19.8$ )

Oral sucker: 37–55 ( $45.6 \pm 3.3$ ) x 37–60 ( $46.8 \pm 3.6$ )  
Ventral sucker: 57–83 ( $69.3 \pm 4.6$ ) x 57–83 ( $66.3 \pm 3.8$ )  
Prepharynx (n=246): 75–148 ( $120.5 \pm 13.1$ )  
Pharynx (n=246): 17–28 ( $23.6 \pm 2.0$ )  
Excretory vesicle: 85–150 ( $115.4 \pm 12.8$ ) x 37–63 ( $49.7 \pm 4.2$ )  
Tail (n=173): 510–950 ( $708.6 \pm 79.3$ ) x 27–53 ( $38.3 \pm 5.1$ )

*Cercarial emergence: rhythm and variation.* Large numbers of cercariae emerged every 2–5 days, sometimes on consecutive days; emergence generally between 7 pm and 8 am.

*Behavior.* Naturally emerged cercariae are free-swimming and swim actively toward light where they orient themselves facing toward the light source. When swimming, the hindbody is folded ventrally and the forebody is contracted longitudinally; the tail lashes from side to side for movement (Figure 2c). When resting, the hindbody is slightly flexed ventrally; tail extends forwards and angled dorsally from hindbody, may be held close to hindbody (Figures 2d). When first emerged, cercariae swim actively towards light and frequently rise to surface; then settle characteristically on their side. After about 24 hours, cercariae become less active, decaudation may occur and they start to die. The cercariae never encyst.

### *Cercaria capricornia III*

(Fig. 3)

**Host:** *Nassarius olivaceus* (Bruguière) (Gastropoda, Nassariidae).

**Locality:** Ross Creek, Yeppoon, Queensland ( $23^{\circ}8' S$ ,  $150^{\circ}45' E$ ).

**Habitat:** Amongst and immediately adjacent to mangroves on intertidal mudflats.

**Prevalence of emergence:** 0.10% (2 of 1908 *N. olivaceus*).

**Material:** South Australian Museum, AHC 29312–AHC 29313, AHC 34549–AHC 34553.

**Dates of collection:** February and November 2005.

#### **Description:**

Redia

*Site.* Reproductive and digestive glands.

*Structure.* Body elongate, cylindrical with posterior extremity tapering to point (Figure 3e). Mouth opens terminally; pharynx spherical. Cercariae in various stages of development.

*Dimensions.* Based on 10 unflattened rediae.

Length: 620–1000 (801.0)

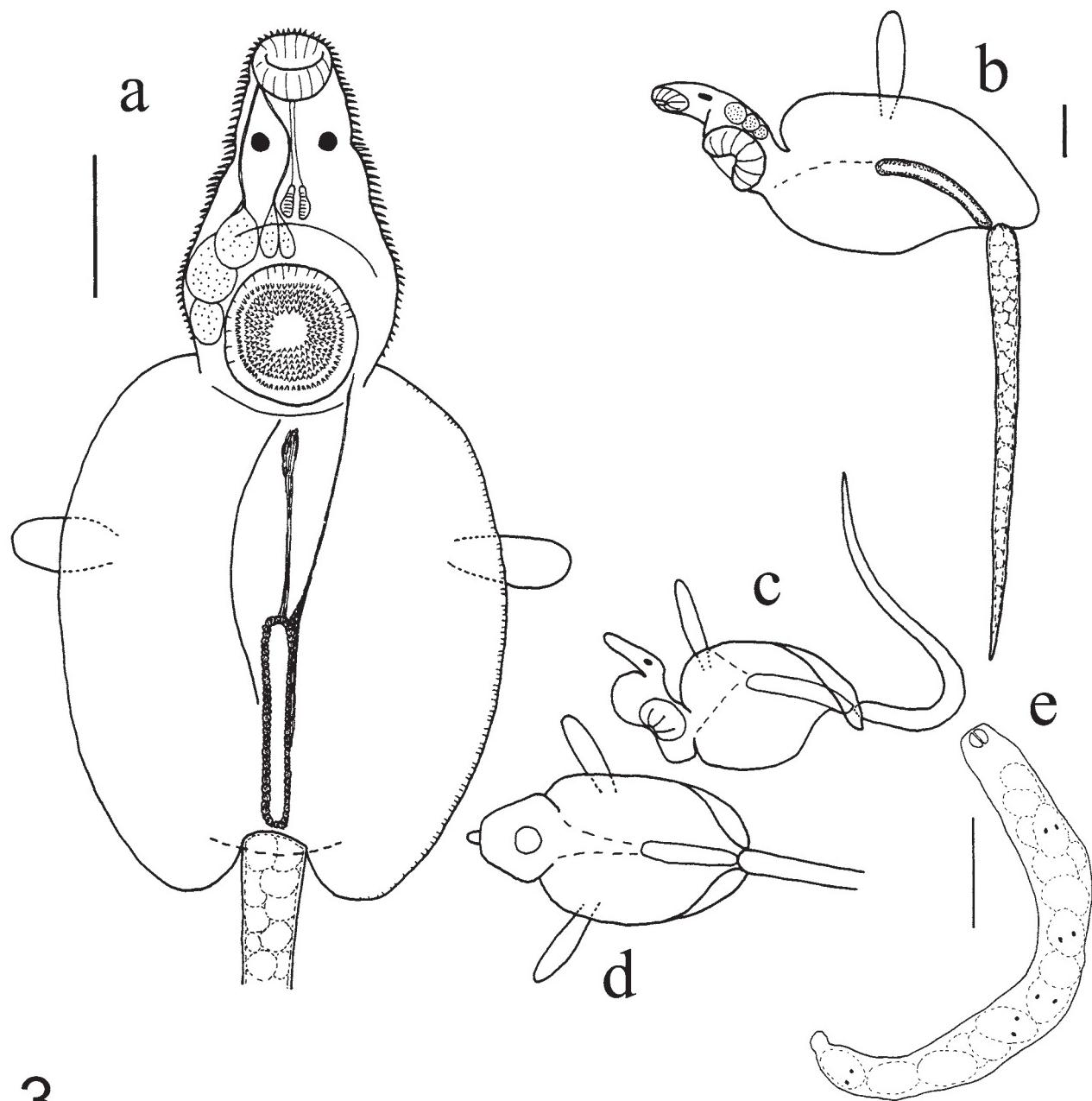
Width: 100–170 (121.0)

Pharynx: 22–30 (25.5) x 20–30 (26.3)

Naturally emerged cercaria

*Body.* Flattened, with conspicuous constriction immediately posterior to ventral sucker (Figure 3a). Forebody reduced, arched ventrally; body anterior to constriction pyriform, widest at level of anterior margin of ventral sucker. Hindbody posterior to constriction expanded, large, broadly ovate, extremely flattened, extending backwards beyond tail junction on both sides, with deep ventral keel longitudinally between constriction and midpoint of excretory vesicle; keel oblong in profile, deepest at anterior margin of excretory vesicle (Figure 3b). In life, body bent dorsally ( $\sim 90^{\circ}$ ) at constriction, forebody bent forward ventrally at eye-spots; fleshy portion around ventral sucker extremely expanded; hindbody bent ventrally ( $\sim 120^{\circ}$ ) at level of anterior margin of excretory vesicle; sides of hindbody anterior from this point to appendage flexed dorsally in a shallow V, sides of posterior hindbody curving ventrally, bowl shaped (Figures 3c, 3d).

*Appendages:* Paired appendages, arising from dorsal surface near lateral edge of hindbody, flat paddle shape variable from short, wide to longer, narrow.



3

**FIGURE 3.** a–e. *Cercaria capricornia* III, naturally emerged from *Nassarius olivaceus*: a. Body, heat-killed, in ventral view; b. Entire cercaria, heat-killed, from side view; c. Live cercaria, resting attitude, side view; d. Live cercaria, resting attitude, ventral view; e. Rediae, fixed, containing cercariae at different stages of development. Scale bars a, b = 100  $\mu\text{m}$ ; c, d not to scale; e = 200  $\mu\text{m}$ .

**Tegument.** Spines anterior to constriction, arranged in regular rows in anterior forebody, longest in anterior two-thirds forebody, decreasing in size towards constriction.

**Suckers.** Oral sucker opening ventrosubterminally, spinose, lacking stylet. Ventral sucker round, row of approximately 93–94 inward pointing spines at aperture, several rows of spines bordering the cavity.

**Eye-spots.** Round, dense, lateral on either side of prepharynx.

**Pigment.** Golden brown shading, throughout hindbody, in fleshy portion anterior to ventral sucker.

**Penetration glands.** Two pairs of small central glands; ducts run anteriorly either side of pharynx, con-

tinue forward medially, diverging laterally anterior to eye-spots and running to dorsal lip of oral sucker; three pairs of large lateral glands present, anterolateral to ventral sucker; ducts run anteriorly on lateral edges of body to dorsal lip of oral sucker; all anterior to constriction.

*Digestive system.* Mouth opens anteroventrally. Prepharynx long, narrow. Pharynx pyriform, small.

*Excretory system.* Excretory vesicle I-shaped, cylindrical, turgid, thin-walled, slightly longer than one-third length hindbody. Two lateral ducts open into anterior extremity of vesicle, continue in close association with vesicle towards posterior extremity. Flame cells difficult to discern, formula not determined.

*Tail.* Simple, long, cylindrical, gradually tapering terminally; lacks spines, setae or fins.

*Dimensions.* Based on 36 naturally emerged specimens.

Total length body: 485–760 (584.6 ± 81.1)

Length anterior end to tail base: 445–700 (541.4 ± 74.9)

Maximum width hindbody: 215–420 (280.7 ± 57.0)

Maximum width forebody: 115–183 (143.5 ± 18.5)

Width at constriction: 70–133 (95.2 ± 16.3)

Length forebody: 125–175 (149.8 ± 12.4)

Oral sucker: 42–53 (48.1 ± 2.8) x 45–53 (48.7 ± 2.1)

Ventral sucker: 77–105 (91.0 ± 7.1) x 75–103 (87.4 ± 7.2)

Prepharynx: 85–120 (104.0 ± 9.1)

Pharynx: 20–25 (22.4 ± 1.7)

Excretory vesicle: 122–220 (157.4 ± 26.9) x 25–35 (27.7 ± 3.0)

Tail: 430–810 (608.2 ± 123.3) x 35–63 (47.8 ± 8.8)

Appendage (n=70): 35–265 (92.4 ± 54.3) x 15–63 (36.7 ± 11.3)

*Cercarial emergence: rhythm and variation.* Large numbers seen to emerge on consecutive days, length of time between periods of emergence not determined.

*Behavior.* Naturally emerged cercariae are free-swimming and swim actively toward light. When swimming, the hindbody is folded ventrally and the forebody is contracted longitudinally, appendages are contracted; the tail lashes from side to side for movement. When resting, the hindbody is held in three-dimensional shape (Figure 3c); tail extends backwards dorsally from hindbody, curves ventrally. When first emerged, cercariae swim actively towards light and frequently rise to surface, float in water column, slowly settle. After about 24 hours, cercariae become less active, may attach to the substrate at tip of tail, decaudation may occur and they start to die. The cercariae never encyst.

#### *Cercaria capricornia* IV

(Fig. 4)

**Host:** *Nassarius olivaceus* (Bruguière) (Gastropoda, Nassariidae).

**Locality:** Sandy Point, Corio Bay (22°58' S, 150°46' E).

**Habitat:** Amongst and immediately adjacent to mangroves on intertidal mudflats.

**Other localities:** Ross Creek, Yeppoon (23°8' S, 150°45' E), Cawarral Creek, Keppel Sands, Queensland (23°19' S, 150°47' E).

**Prevalence of emergence:** 0.31% (6 of 1908 *N. olivaceus*).

**Material:** South Australian Museum, AHC 29314–AHC 29316, AHC 34554–AHC 34564.

**Dates of collection:** August 2004, May/August 2005 and February 2006.

**Description:**

Redia

*Site.* Reproductive and digestive glands.

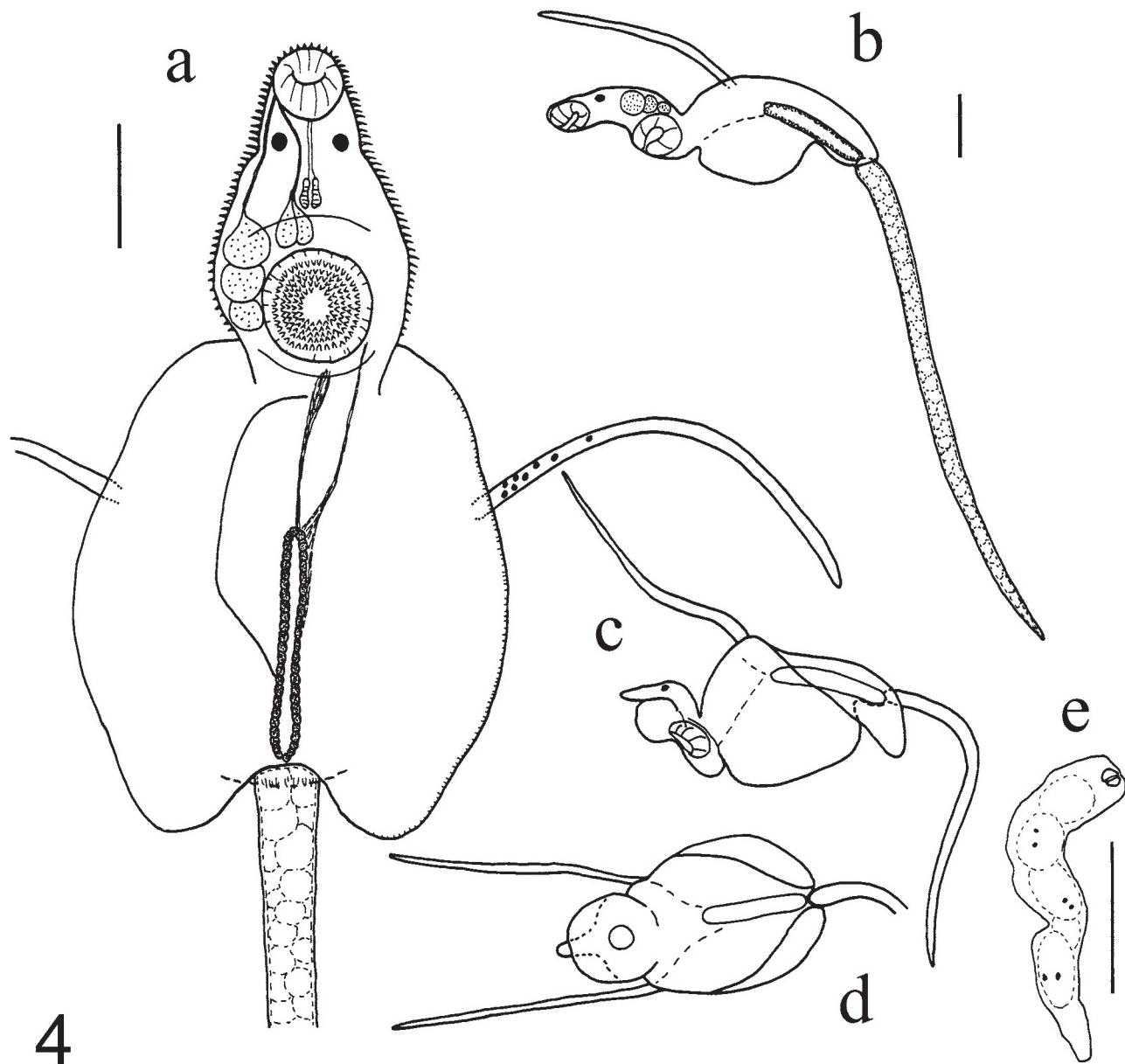
*Structure.* Body elongate, cylindrical with posterior extremity tapering to point (Figure 4e). Mouth opens terminally; pharynx spherical. Cercariae in various stages of development.

*Dimensions.* Based on 10 unflattened rediae.

Length: 400–510 (468.0)

Width: 70–110 (86.0)

Pharynx: 20–23 (21.0) x 17–23 (20.5)



**FIGURE 4.** a–e. *Cercaria capricornia* IV, naturally emerged from *Nassarius olivaceus*: **a.** Body, heat-killed, in ventral view; **b.** Entire cercaria, heat-killed, from side view; **c.** Live cercaria, resting attitude, side view; **d.** Live cercaria, resting attitude, ventral view; **e.** Rediae, fixed, containing cercariae at different stages of development. Scale bars a, b = 100 µm; c, d not to scale; e = 200 µm.

#### Naturally emerged cercaria

*Body.* Flattened, with conspicuous constriction immediately posterior to ventral sucker (Figure 4a). Forebody reduced, arched ventrally; body anterior to constriction pyriform, widest at level of anterior margin of

ventral sucker. Hindbody posterior to constriction expanded, large, broadly ovate, extremely flattened, extending backwards beyond tail junction on both sides, with very deep ventral keel longitudinally between constriction and midpoint of excretory vesicle; keel oblong in profile, deepest at anterior margin of excretory vesicle (Figure 4b). In life, body bent dorsally at constriction ( $\sim 90^\circ$ ), forebody bent forward ventrally at eye-spots; fleshy portion around ventral sucker extremely expanded; hindbody bent ventrally ( $\sim 120^\circ$ ) at level of anterior margin of excretory vesicle; sides of hindbody anterior from this point flexed dorsally in a shallow V; sides of posterior hindbody curving ventrally, bowl shaped (Figure 4c, 4d).

*Appendages*: Long tubular filament-like appendages arising from dorsal surface of hindbody at level slightly forward of anterior margin of excretory vesicle and near to margin of body. Extremely extensible, more extended in live cercariae.

*Tegument*. Spines anterior to constriction, arranged in regular rows in anterior forebody, longest in anterior two-thirds forebody, decreasing in size towards constriction.

*Suckers*. Oral sucker opening ventrosubterminally, spinose, lacking stylet. Ventral sucker round, row of 87–98 inward pointing spines at aperture, several rows of spines bordering cavity.

*Eye-spots*. Round, dense, lateral on either side of prepharynx.

*Pigment*. Variable, faint to dark golden brown or red brown shading throughout body; often darker anterior and posterior to ventral sucker and along fold of keel; conspicuous red brown rectangular patches on hindbody beside base of tail may be present. In life, translucent to bright pinkish/orange; blue pigmentation on keel and fleshy portion around ventral sucker may be present.

*Penetration glands*. Possibly two pairs of small central glands; ducts run anteriorly either side of pharynx, continue forward medially; possibly three pairs of large lateral glands present, anterolateral to ventral sucker; ducts run anteriorly on lateral edges of body; difficult to determine; all anterior to constriction.

*Digestive system*. Mouth opens anteroventrally. Prepharynx long, narrow. Pharynx pyriform, small. Pharynx difficult to determine in specimens from one host, obscured by dark pigmentation.

*Excretory system*. Excretory vesicle I-shaped, cylindrical, turgid, thin-walled, slightly longer than one-third length hindbody. Two lateral ducts open into anterior extremity of vesicle, continue in close association with vesicle towards posterior extremity. Flame cells difficult to discern, formula not determined.

*Tail*. Simple, long, cylindrical, gradually tapering terminally; lacks spines, setae or fins.

*Dimensions*. Based on 83 naturally emerged specimens.

Total length body: 580–870 (728.6  $\pm$  75.4)

Length anterior end to tail base: 540–810 (675.8  $\pm$  72.7)

Maximum width hindbody: 280–400 (342.7  $\pm$  33.5)

Maximum width forebody: 125–215 (173.3  $\pm$  14.0)

Width at constriction (n=68): 55–138 (103.3  $\pm$  20.3)

Length forebody: 137–218 (175.7  $\pm$  21.4)

Oral sucker: 47–60 (52.1  $\pm$  2.9) x 45–63 (52.6  $\pm$  4.2)

Ventral sucker: 82–113 (100.4  $\pm$  6.0) x 82–105 (94.8  $\pm$  5.2)

Prepharynx (n=63): 90–140 (118.5  $\pm$  11.0)

Pharynx (n=62): 17–30 (24.0  $\pm$  2.4)

Excretory vesicle: 175–270 (224.3  $\pm$  20.0) x 22–38 (28.2  $\pm$  3.4)

Tail (n=80): 690–990 (824.9  $\pm$  81.6) x 42–68 (51.6  $\pm$  5.5)

Appendage (n=163): 155–790 (453.6  $\pm$  127.9) x 12–28 (18.4  $\pm$  2.9)

*Cercarial emergence: rhythm and variation*. Few to large numbers emerged between 7 pm and 8 am; 1–6 days between periods of emergence, emerged on consecutive days (recorded for 9 consecutive days with only 5–42 cercariae emerging for last 4 days).

*Behavior*. Naturally emerged cercariae are free-swimming and swim actively toward light. When swimming, the hindbody is folded ventrally and forebody contracted longitudinally; the tail lashes from side to side

for movement. When resting, the hindbody is held in three-dimensional shape, tail extends backwards dorsally from hindbody, curves ventrally (Figure 4c). When first emerged, cercariae swim actively towards light and frequently rise to surface, float in water column, slowly settle. After about 24 hours, cercariae become less active, may attach to the substrate at tip of tail, decaudation may occur and they start to die. The cercariae never encyst.

### *Cercaria capricornia* V

(Fig. 5)

**Host:** *Nassarius dorsatus* (Röding) (Gastropoda, Nassariidae).

**Locality:** Cawarral Creek, Keppel Sands, Queensland (23°19' S, 150°47' E).

**Habitat:** Intertidal mudflats.

**Prevalence of emergence:** 0.06% (1 of 1766 *N. dorsatus*).

**Material:** South Australian Museum, AHC 29317, AHC 34565–AHC 34566.

**Date of collection:** 16 August, 2004.

#### **Description:**

Redia

*Site.* Reproductive and digestive glands.

*Structure.* Body elongate, cylindrical with posterior extremity tapering to point (Figure 5e). Mouth opens terminally; pharynx spherical. Cercariae in various stages of development.

*Dimensions.* Based on 10 unflattened rediae.

Length: 490–810 (617.0)

Width: 45–70 (54.5)

Pharynx: 17–23 (20.0) x 17–20 (19.3)

#### Naturally emerged cercaria

*Body.* Flattened, with conspicuous constriction immediately posterior to ventral sucker (Figure 5a). Forebody reduced, arched ventrally; body anterior to constriction pyriform, widest at level of anterior margin of ventral sucker. Hindbody posterior to constriction expanded, large, broadly ovate, extremely flattened, extending backwards beyond tail junction on both sides, with very deep ventral keel longitudinally between constriction and midpoint of excretory vesicle; keel oblong in profile, deepest at anterior margin of excretory vesicle (Figure 5b). In life, body bent dorsally at constriction (~105°), forebody bent forward ventrally at eye-spots; fleshy portion around ventral sucker extremely expanded; hindbody bent ventrally (~130°) at level of anterior margin of excretory vesicle; anterior sides of hindbody from this point to appendage flexed dorsally in a shallow V, posterior hindbody almost in single plane with sides curving slightly ventrally, shallowly bowl shaped (Figure 5c, 5d).

*Appendages:* Long tubular filament-like appendages arising from dorsal surface of hindbody at level slightly forward of anterior extremity of excretory vesicle and near margin of body. Extremely extensible, more extended in live cercariae.

*Tegument.* Spines anterior to constriction, arranged in regular rows in anterior forebody, longest in anterior two-thirds forebody, decreasing in size towards constriction.

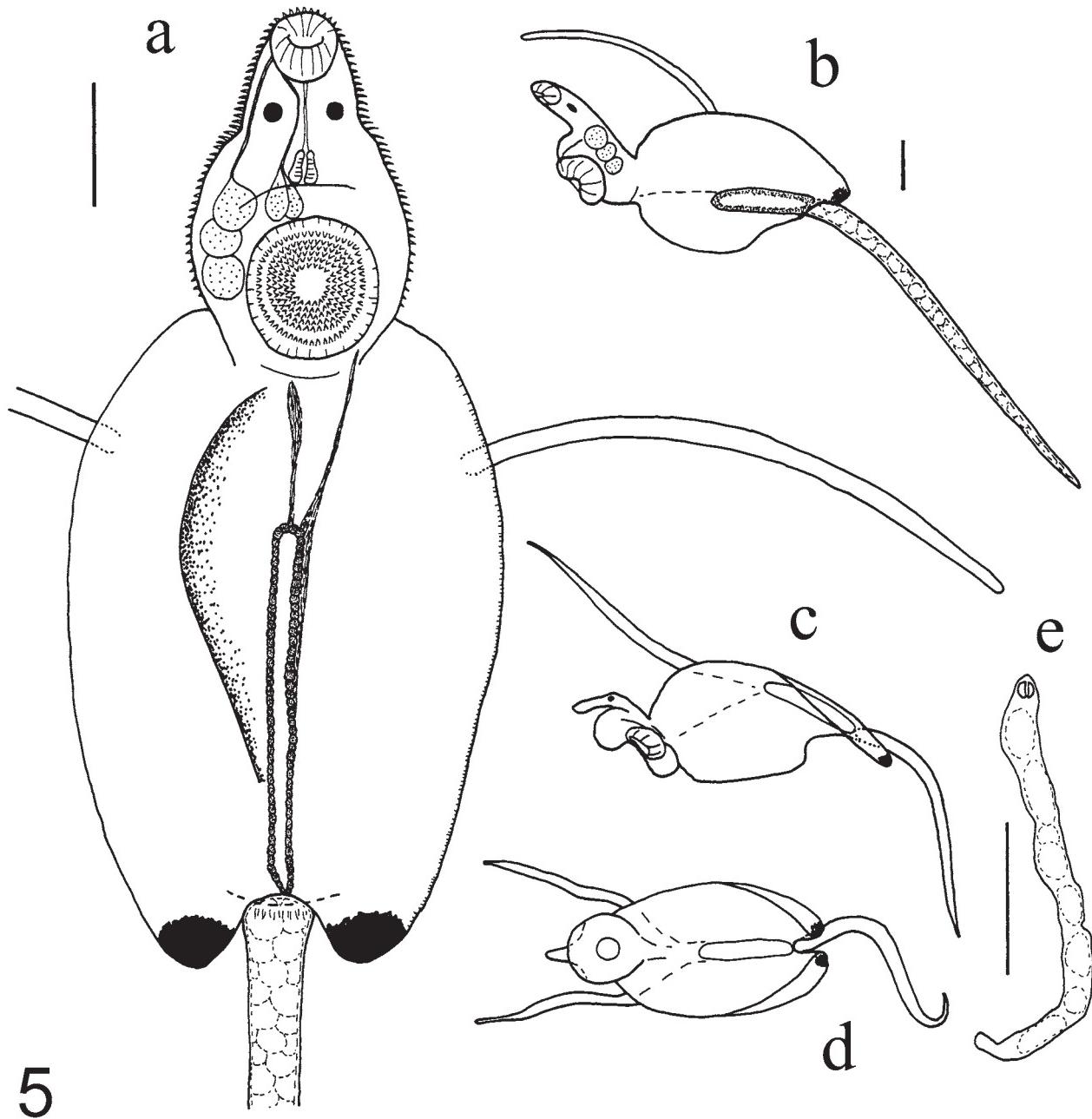
*Suckers.* Oral sucker opening ventrosubterminally, spinose, lacking stylet. Ventral sucker round, row of approximately 86–88 inward facing spines at aperture, several rows of spines bordering cavity.

*Eye-spots.* Round, dense, lateral on either side of prepharynx.

*Pigment.* Red brown, dense, conspicuous, on posterior extremity of hindbody either side of tail base, oval in shape; red brown, diffuse, anterior from base of tail by about one-third length excretory vesicle; golden

brown, diffuse shading, in fleshy portion anterior to ventral sucker, over keel and anterior and posterior areas of hindbody. In life, body white with bright orange spots on posterior extremity.

*Penetration glands.* Two pairs of small central glands; ducts run anteriorly either side of pharynx, continue forward medially; possibly three pairs of large lateral glands present, difficult to determine, anterolateral to ventral sucker; ducts run anteriorly on lateral edges of body; all anterior to constriction.



**FIGURE 5.** a–E. *Cercaria capricornia* V, naturally emerged from *Nassarius dorsatus*: **a**. Body, heat-killed, in ventral view; **b**. Entire cercaria, heat-killed, from side view; **c**. Live cercaria, resting attitude, side view; **d**. Live cercaria, resting attitude, ventral view; **e**. Rediae, fixed, containing cercariae at different stages of development. Scale bars a, b = 100 µm; c, d not to scale; e = 200 µm.

*Digestive system.* Mouth opens anteroventrally. Prepharynx long, narrow. Pharynx pyriform, small.

*Excretory system.* Excretory vesicle I-shaped, cylindrical, turgid, thin-walled, about half length hindbody. Two lateral ducts open into anterior extremity of vesicle, continue in close association with vesicle towards

posterior extremity. Flame cells difficult to discern, formula not determined.

*Tail*. Simple, long, cylindrical, gradually tapering terminally; lacks spines, setae or fins.

*Dimensions*. Based on 10 naturally emerged specimens.

Total length body: 700–870 (770.0)

Length anterior end to tail base: 650–800 (720.0)

Maximum width hindbody: 320–370 (345.0)

Maximum width forebody: 167–183 (177.0)

Length forebody: 162–200 (179.8)

Oral sucker: 50–58 (53.8) x 52–58 (54.3)

Ventral sucker: 105–115 (112.3) x 100–108 (103.5)

Prepharynx: 105–125 (114.3)

Pharynx: 20–25 (23.5)

Excretory vesicle: 260–315 (289.5) x 25–38 (27.5)

Tail: 850–900 (875.5) x 50–60 (56.5)

Appendage: (n=20): 270–770 (451.0) x 15–20 (17.5)

*Cercarial emergence: rhythm and variation*. Large numbers emerge with a few days between emergences.

*Behavior*. Naturally emerged cercariae are free-swimming and swim actively toward light. When resting, the hindbody is flexed ventrally; tail extends backwards dorsally from hindbody, curved ventrally (Figure 5c). When first emerged, cercariae swim actively towards light and frequently rise to surface, float in water column, slowly settle. After about 24 hours, cercariae become less active, may attach to the substrate at tip of tail, decaudation may occur and they start to die. The cercariae never encyst.

### *Cercaria capricornia VI*

(Fig. 6)

**Host:** *Nassarius dorsatus* (Röding) (Gastropoda, Nassariidae).

**Locality:** Sandy Point, Corio Bay, Queensland (22°58' S, 150°46' E).

**Habitat:** Intertidal mudflats.

**Prevalence of emergence:** 0.06% (1 of 1766 *N. dorsatus*).

**Material:** South Australian Museum, AHC 29318, AHC 34567–AHC 34568.

**Date of collection:** 15 August, 2004.

#### **Description:**

Redia

*Site*. Reproductive and digestive glands.

*Structure*. Body elongate, cylindrical with posterior extremity tapering to rounded point (Figure 6c).

Mouth opens terminally; pharynx spherical. Cercariae in various stages of development.

*Dimensions*. Based on 10 unflattened rediae.

Length: 340–470 (422.0)

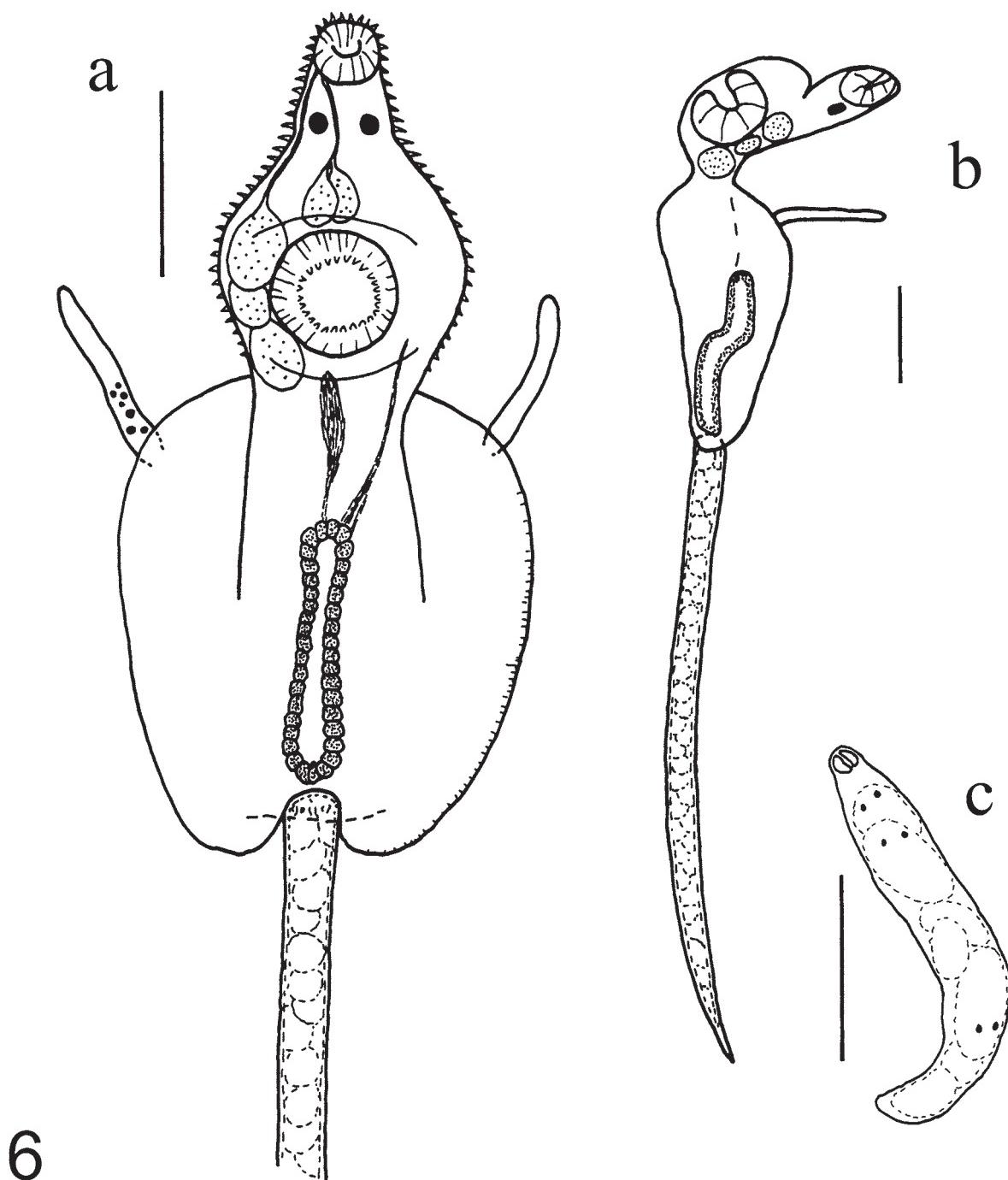
Width: 60–80 (72.0)

Pharynx: 20–25 (22.5) x 20–23 (21.5)

#### Naturally emerged cercaria

*Body*. Flattened, with conspicuous constriction immediately posterior to ventral sucker (Figure 6a). Forebody reduced, expanded immediately anterior to ventral sucker, angled 90° dorsally from posterior hindbody at constriction; body anterior to constriction pyriform, widest at level of anterior margin of ventral sucker. Hindbody posterior to constriction expanded, large, broadly ovate, extremely flattened, extending backwards

beyond tail junction on both sides, with shallow, wide ventral keel longitudinally between constriction and posterior hindbody, keel virtually a cylindrical expansion (Figure 6b). Conformation of live cercariae not documented.



**FIGURE 6.** a–c. *Cercaria capricornia* VI, naturally emerged from *Nassarius dorsatus*: a. Body, heat-killed, in ventral view; b. Entire cercaria, heat-killed, from side view; c. Rediae, fixed, containing cercariae at different stages of development. Scale bars a, b = 100 µm; c = 200 µm.

**Appendages:** Long tubular filament-like appendages arising from dorsal surface of hindbody at level slightly forward of anterior extremity of excretory vesicle and near margin of body, projecting anterolaterally.

**Tegument.** Spines anterior to constriction, arranged in regular rows in anterior forebody, longest in anterior two-thirds forebody, decreasing in size towards constriction.

**Suckers.** Oral sucker opening ventrosubterminally, spinose, lacking stylet. Ventral sucker round, aperture

surrounded by single row of 66–81 inwardly facing minute spines.

*Eye-spots*. Round, dense, lateral on either side of prepharynx.

*Pigment*. Live cercariae, white.

*Penetration glands*. Central and lateral glands present, unable to be determined, lateral glands may extend posteriorly from ventral sucker.

*Digestive system*. Mouth opens anteroventrally. Prepharynx and pharynx unable to be determined.

*Excretory system*. Excretory vesicle I-shaped, cylindrical, turgid, with cuboidal cells, about two-fifths length hindbody. Two lateral ducts open into anterior extremity of vesicle. Flame cells difficult to discern, formula not determined.

*Tail*. Simple, long, cylindrical, gradually tapering terminally; lacks spines, setae or fins.

*Dimensions*. Based on 10 naturally emerged specimens.

Total length body: 400–460 (431.0)

Length anterior end to tail base: 370–430 (398.0)

Maximum width hindbody: 210–265 (238.8)

Maximum width forebody: 110–145 (128.0)

Width at constriction (n=9): 55–88 (74.7)

Length forebody: 102–120 (113.0)

Oral sucker: 35–40 (36.0) x 35–40 (38.0)

Ventral sucker: 67–73 (69.5) x 67–75 (71.5)

Excretory vesicle: 115–150 (133.3) x 25–35 (30.5)

Tail: 580–660 (624.5) x 25–38 (31.0)

Appendage (n=20): 30–205 (110.9) x 10–15 (12.8)

*Cercarial emergence: rhythm and variation*. These cercariae emerged in highly variable numbers, with 1–3 observed to emerge for up to 4 consecutive days, with breaks of approximately 3–7 days between emergences; two emergences of >100 cercariae were also observed.

*Behavior*. Naturally emerged cercariae are free-swimming and swim actively toward light.

## Discussion

### Affinities

The cercariae described here are conditionally identified as Acanthocolpidae on the basis of their dorsoventrally flattened body, spinose tegument, ventrally subterminal oral sucker, pre-equatorial ventral sucker, long prepharynx, pyriform pharynx and I-shaped excretory vesicle, characters in agreement with the definition of the family as proposed by Bray (2005). Families to whose cercariae they show some resemblance include Lepocreadiidae and Apocreadiidae but they differ from both principally in lacking setiferous tails.

The cercariae reported here resemble to some extent a number of other large distinctive cercariae that have also been attributed to the Acanthocolpidae: *Cercaria caribbea* XXXIV Cable, 1956, *C. portosacculus* Holliman, 1961, *C. caribbea* LXXII Cable, 1963, *C. caribbea* LXXIII Cable, 1963, *C. itoi* Shimura, 1984 and a probable *Tormopsolus* cercaria (Bartoli & Gibson 1998, Cable 1956, Cable 1963, Holliman 1961, Shimura 1984). Of these, the most significant resemblance is that to *C. itoi* and the cercaria from *Cantharus dorbignyi* which Bartoli and Gibson (1998) argued convincingly were both likely to be species of the acanthocolpid genus *Tormopsolus*. The similarity includes a large body that has a spiny tegument, well-developed oral and ventral suckers, eye-spots, absence of a stylet, presence of penetration glands and a simple tail lacking fins or setae.

*Cercariae capricornia* I–VI differ from the cercariae listed above in their three-dimensional body shape, featuring a conspicuous constriction near the ventral sucker, an extremely flattened and expanded hindbody

and a ventral keel. They lack the caudal bulb of *C. caribbea* XXXIV, *C. portosacculus*, *C. caribbea* LXXII and *C. caribbea* LXXIII (Cable 1956, Cable 1963, Holliman 1961), and the keel does not appear analogous to the fleshy protuberance surrounding the ventral suckers of *C. caribbea* LXXII, *C. caribbea* LXXIII and *C. itoi* (Cable 1963, Shimura 1984). The swimming action of the six Australian species, involving the hindbody folded ventrally, differs from that of *C. itoi* and the putative *Tormopsolus* cercaria, which have the hindbody contracted but not folded (Bartoli & Gibson 1998, Shimura 1984). Although the hindbody of *C. portosacculus* and the putative *Tormopsolus* cercaria is greatly expanded, the shape is more ovoid and without a conspicuous constriction (Holliman 1961, Shimura 1984).

The putative acanthocolpid cercariae reported previously have all been reported from gastropods of the superfamily Muricoidea (Buccinidae, Columbellidae and Fasciolariidae). The present cercariae infected another muricoid family, the Nassariidae. On the basis of the similarity to previously reported forms in morphology and host we hypothesise that the new forms here also belong to the Acanthocolpidae.

The discovery of a complex of six species raises interesting questions as to the species and genus level identity of these forms. The acanthocolpid fauna of Australian fishes is rich. There are presently four species of *Monostephanostomum* (Bray & Cribb 2002, Bray & Cribb 2007a, Kruse 1979), one species of *Ningalooia* (Bray & Cribb 2007b), one species of *Pleorchis* (Bray 2005), 12 species of *Stephanostomum* (Bray 2005, Bray & Cribb 2003, Bray & Cribb 2004, Bray & Cribb 2006, Hutson *et al.* 2007, Korotaeva 1970, Korotaeva 1975, Korotaeva 1982, Lester & Sewell 1990), two species of *Tormopsolus* (Bartoli *et al.* 2004, Bray & Cribb 2001, Hutson *et al.* 2007) and one species of *Venusicola* (Bray & Cribb 2000) known from Australian waters. Given that there are six similar species of cercariae reported here, it is tempting to predict that they will belong to the largest of these genera, *Stephanostomum*.

There are four probable acanthocolpid cercariae reported previously from nassariid gastropods: three species of *Stephanostomum*, those of *S. tenue* (Linton) and *S. dentatum* (Linton) from *N. obsoletus* (Say) (see Martin 1939, Stunkard 1961) and *S. cloacum* (Srivastava) from *N. orissaensis* (Preston) (see Madhavi & Shameem 1993); and *Cercaria bengalensis* VIII Gnana Mani from *N. stolatus* (Gmelin), which was described as closely resembling the cercariae of *S. tenue* and *S. caducum* (Looss) (Gnana Mani 1994). These four cercariae have a simpler body shape (Gnana Mani 1994, Madhavi & Shameem 1993, Martin 1939, Stunkard 1961) in that they do not share the distinctive features of the six Australian species (three-dimensional body shape, conspicuous constriction near the ventral sucker, extremely flattened and expanded hindbody and ventral keel). Thus, it is far from clear that the new Australian cercariae will relate to species of *Stephanostomum*.

It is possible that these species relate to the family Brachycladiidae (synonym Campulidae) which are mainly parasites of marine mammals. Several studies (see Bray *et al.* 2005) have shown that the Brachycladiidae is genetically close to the Acanthocolpidae and may have arisen from within it. Brachycladiids are common mainly in toothed whales. Although there are almost no published records of brachycladiids from cetaceans in Australian waters (McColl & Obendorf 1982), there is little doubt that the group will prove to be rich as there is a rich fauna of toothed whales there. It is thus possible that these cercariae will prove to be those of brachycladiids but resolution of this issue will probably require a DNA sequencing approach.

Given that none of the cercariae in this study encysted in the open, it seems likely that transmission (presumably to fishes) occurs either by penetration or ingestion. The bright pigmentation, complex body shapes, appendages and active swimming action may attract the attention of fish and other grazing animals by imitating microfauna normally consumed, in a similar way to that suggested by Bartoli and Gibson (1998) for the putative *Tormopsolus* cercaria.

#### Distinction of cercariae

The six forms reported here show considerable general similarity to each other, but are distinguishable as follows. Two of the species, *C. capricornia* I and *C. capricornia* II, lack body appendages and have a less complex body shape than those with appendages, with the sides of the hindbody flexed dorsally into a V

shape. Both cercariae also have oblong eye-spots, one row of spines at the aperture of the ventral sucker, three pairs of penetration glands in the hindbody, no penetration glands evident in the forebody, a thick-walled excretory vesicle and no appendages on the hindbody. They differ from each other in that *C. capricornia* I has conspicuous pigmentation in the forebody, and conformation of the body and placement of the tail in live cercariae differ slightly but consistently from that of *C. capricornia* II. There are also behavioral differences in that *C. capricornia* I orients away from light and *C. capricornia* II orients towards it.

*Cercariae capricornia* III–V have a more complex body shape than *C. capricornia* I and II, in that the hindbody is bent transversely at about the anterior margin of the excretory vesicle, the sides of the anterior hindbody reflex dorsally in a shallow V shape, and the posterior hindbody curves ventrally into a bowl shape. They also have round eye-spots, multiple rows of spines within the ventral sucker cavity, all penetration glands anterior to the constriction (and the presence of central glands, which are absent or greatly reduced and not evident in *C. capricornia* I and II), a thin-walled excretory vesicle and appendages on the hindbody. *Cercaria capricornia* III has a pair of uniquely identifying flat paddle-like appendages that arise on the dorsal edge of the hindbody and are less than a third of the body length, whereas *C. capricornia* IV and V have a pair of long tubular filament-like appendages of variable length, often more than half as long as the body. *Cercaria capricornia* V has the excretory vesicle marginally longer relative to the body length and hindbody length than in *C. capricornia* IV, conspicuous dense pigment on the hindbody at the posterior extremity either side of the tail base and a slightly different conformation of the body in live cercariae with more obtuse angles at the bends of the body (at constriction ~105° compared to ~90° in *C. capricornia* IV, and at mid hindbody ~130° compared to ~120°). The curvature of the posterior hindbody is shallower than in *C. capricornia* IV. *Cercariae capricornia* III and IV emerged from *N. olivaceus* whilst *C. capricornia* V emerged from *N. dorsatus*.

*Cercaria capricornia* VI closely resembles *C. capricornia* III–V, in having the complex body shape, but differs in having only a single row of minute spines at the aperture of the ventral sucker, penetration glands that extend posterior to the ventral sucker and an excretory vesicle with cuboidal cells of width medial between that of *C. capricornia* I and II and that of *C. capricornia* III–V.

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